1 **Title:** Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate
2 broadleaf forest

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Summary

- As climate change is driving increased drought frequency and severity in many forested regions around the world, mechanistic understanding of the factors conferring drought resistance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and species' traits shape tree growth responses during droughts.

- We analyzed tree-ring records for twelve species that comprise 97% of the woody productivity of the 25.6-ha ForestGEO plot in a broadleaf deciduous forest of northern Virginia (USA) to test hypotheses on how tree height, microenvironment characteristics, and species' traits shaped drought responses across the three strongest regional droughts over a 60-year period (1950 - 2009).

- Individual-level drought resistance decreased with tree height, which was strongly correlated with exposure to higher evaporative demand and solar radiation. The potentially greater rooting volume of larger trees did not confer an advantage in sites with low topographic wetness index. Resistance was greater among species whose leaves experienced less shrinkage upon desiccation and lost turgor (wilted) at more negative water potentials.

- We conclude that tree height and leaf drought tolerance traits influence growth responses during drought, as recorded in the tree-ring record spanning historical droughts. Thus, these factors can be useful for predicting future drought responses under climate change.

Introduction

Forests play a critical global role in climate regulation (Bonan, 2008), yet there remains enormous uncertainty as to how the forest-dominated terrestrial carbon sink will respond to climate change (Friedlingstein et al., 2006). An important aspect of this uncertainty lies with physiological responses of trees to drought (Kennedy et al., 2019). In many forested regions around the world, the risk of severe drought is increasing (Trenberth et al., 2014; Dai et al., 2018), often despite increasing precipitation (Intergovernmental Panel on Climate Change, 2015; Cook et al., 2015). Droughts, intensified by climate change, have been affecting forests worldwide and are expected to continue as one of the most important drivers of forest change in the future (Allen et al., 2010, 2015). Understanding forest responses to drought requires elucidation of how tree size, microenvironment, and species' traits jointly influence individual-level drought resistance, defined here as a tree's ability to maintain growth during drought, and the extent to which their influence is consistent across droughts. Because the resistance and resilience (i.e., post-drought recovery) of growth to drought are linked to trees' probability of surviving drought (DeSoto et al., 2020; Liu et al., 2019), understanding growth responses can also help elucidate which trees are most vulnerable to drought-induced mortality. However, it has proven difficult to resolve the many factors affecting tree growth during drought with available forest census data, which only rarely captures extreme drought, and with tree-ring records, which capture multiple droughts but usually only sample a subset of a forest community, typically focusing on a single species or the largest individuals.

Many studies have shown that within and across species, large trees tend to be more affected by drought. Greater growth reductions for larger trees were first shown on a global scale by Bennett et al. (2015), and subsequent studies have reinforced this finding (*e.g.*, Hacket-Pain et al., 2016; Gillerot et al., 2020). It has yet to be resolved which of several potential underlying mechanisms most strongly shape these trends in drought response. First, tree height itself may be a primary driver. Taller trees face the biophysical challenge of lifting water greater distances against the effects of gravity and friction (McDowell et al., 2011; McDowell and Allen, 2015; Ryan et al., 2006; Couvreur et al., 2018). Vertical gradients in stem and leaf traits–including smaller and thicker leaves (higher leaf mass per area, LMA), greater resistance to hydraulic dysfunction (*i.e.*, more negative water potential at 50% loss of hydraulic conductivity, more negative P50), and lower hydraulic conductivity at greater heights (Couvreur et al., 2018; Koike et al., 2001; McDowell et al., 2011)–enable trees to become tall (Couvreur et al., 2018). Greater stem capacitance (*i.e.*, water storage capacity) of larger trees may also confer resistance to transient droughts (Phillips et al., 2003; Scholz et al., 2011). Indeed, tall trees require xylem of greater hydraulic efficiency, such that xylem conduit diameters are wider in the basal portions of taller trees, both within and across species (Olson et al., 2018; Liu et al., 2019), and throughout the conductive systems of angiosperms (Zach et al., 2010; Olson et al., 2014, 2018). Wider xylem conduits plausibly make large trees more vulnerable to embolism during drought (Olson et al., 2018), and traits conducive to efficient water transport may also lead to poor ability to recover from or re-route water around embolisms (Roskilly et al., 2019).

Larger trees may also have lower drought resistance because of microenvironmental and ecological factors. Their crowns tend to occupy more exposed canopy positions, which are associated with higher evaporative demand (Kunert et al., 2017). Subcanopy trees tend to fare better specifically due to the benefits of a buffered environment (Pretzsch et al., 2018). Counteracting the liabilities associated with tall height, large trees tend to have larger root systems (Enquist and Niklas, 2002), potentially mitigating some of the biophysical challenges they face by allowing greater access to water. Larger root systems–if they grant access

to deeper water sources–would be particularly advantageous in drier microenvironments (e.g., hilltops, as compared to valleys and streambeds) during drought. Finally, tree size-related responses to drought can be modified by species' traits and their distribution across size classes (Meakem et al., 2018; Liu et al., 2019). Understanding the mechanisms driving the greater relative growth reductions of larger trees during drought requires sorting out the interactive effects of height and associated exposure, root water access, and species' traits.

Debates have also arisen regarding the traits influencing tree growth responses to drought. Studies within temperate broadleaf forests have observed ring-porous species showing higher drought tolerance than diffuse-porous species (Friedrichs et al., 2009; Elliott et al., 2015; Kannenberg et al., 2019), but this distinction does not always hold (Martin-Benito and Pederson, 2015) and would not hold in the global context (Wheeler et al., 2007; Olson et al., 2020) and does not resolve differences among the many species within each category. Commonly-measured traits including wood density and leaf mass per area (LMA) have been linked to drought responses within some temperate deciduous forests (Abrams, 1990; Guerfel et al., 2009; Hoffmann et al., 2011; Martin-Benito and Pederson, 2015) and across forests worldwide (Greenwood et al., 2017). However, in other cases these traits could not explain drought tolerance (e.g., in a tropical rainforest; Maréchaux et al., 2019), or the direction of response was not always consistent. For instance, higher wood density has been associated with greater drought resistance at a global scale (Greenwood et al., 2017), but correlated negatively with tree performance during drought in a broadleaf deciduous forest in the southeastern United States (Hoffmann et al., 2011). Thus, the perceived influence of these traits on drought resistance may actually reflect indirect correlations with other traits that more directly drive drought responses (Hoffmann et al., 2011).

In contrast, hydraulic traits have direct physiological linkages to tree growth and mortality responses to drought. For instance, water potentials at which percent the loss of conductivity surpasses a certain threshold (e.g., P50 and P88, representing 50 and 88% loss of conductivity, respectively) and hydraulic safety margin (*i.e.*, difference between typical minimum water potentials and P50 or P88) correlate with drought performance across global forests (Anderegg et al., 2016). However, these are time-consuming to measure and therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics). More easily-measurable leaf drought tolerance traits that have direct linkage to plant hydraulic function can explain variation in plant distribution and function (Medeiros et al., 2019). These include leaf area shrinkage upon desiccation (PLA_{dry}; Scoffoni et al., 2014) and the leaf water potential at turgor loss point (π_{tlp}), *i.e.*, the water potential at which leaf wilting occurs (Bartlett et al., 2016a; Zhu et al., 2018). Both traits correlate with hydraulic vulnerability and drought tolerance as part of unified plant hydraulic systems (Scoffoni et al., 2014; Bartlett et al., 2016a; Zhu et al., 2018; Farrell et al., 2017). The abilities of both PLA_{dry} and π_{tlp} to explain tree drought resistance remains untested.

Here, we examine how tree height, microenvironment characteristics, and species' traits collectively shape drought resistance, defined as the ratio of annual growth in a drought year to that which would be expected in the absence of drought based on previous years' growth. We test a series of hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from the three strongest droughts over a 60-year period (1950 - 2009), species trait measurements, and census and microenvironmental data from a large forest dynamics plot in Virginia, USA. First, we focus on how tree size, alone and in its interaction with microenvironmental gradients, influences drought resistance. We examine the contemporary relationship between tree height and microenvironment, including growing season meteorological conditions

125 and crown exposure. We then test whether, consistent with most forests globally, larger-diameter, taller trees
126 tend to have lower drought resistance in this forest, which is in a region (eastern North America) represented
127 by only two studies in the global review of Bennett et al. (2015). We also test for an influence of potential
128 access to available soil water, which should be greater for larger trees in dry but not in perpetually wet
129 microsites. Finally, we focus on the role of species' traits, testing the hypothesis that species'
130 traits--particularly leaf drought tolerance traits--predict drought resistance. We test predictions that
131 drought resistance is higher in ring-porous than semi-ring and diffuse-porous species and that it is correlated
132 with wood density–either positively (Greenwood et al., 2017) or negatively (Hoffmann et al., 2011) and
133 positively correlated with LMA. We further test predictions that species with low PLA_{dry} have higher
134 drought resistance, and that species whose leaves lose turgor lower water potentials (more negative π_{tlp}) have
135 higher resistance.

Materials and Methods

Study site and microclimate

138 Research was conducted at the 25.6-ha ForestGEO (Forest Global Earth Observatory) study plot at the
139 Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W; Fig. **S1**)
140 (Bourg et al., 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains
141 near the northern boundary of Shenandoah National Park. Elevations range from 273 to 338 m above sea
142 level with a topographic relief of 65m (Bourg et al., 2013). Climate is humid temperate, with mean annual
143 temperature of 12.7°C and precipitation of 1005 mm yr⁻¹ during our study period (1960-2009; source: CRU
144 TS v.4.01; Harris et al., 2014). Dominant tree taxa within this secondary forest include *Liriodendron*
145 *tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.; Table 2).

Identifying drought years

147 We identified the three largest droughts within the time period 1950-2009, defining drought (Slette et al.,
148 2019) as events with anomalously dry peak growing season climatic conditions. Specifically, we used the
149 metric of Palmer Drought Severity Index (PDSI) during May-August (MJJA; Table S1), which were
150 identified by Helcoski et al. (2019) as the months of the current year to which annual tree growth was most
151 sensitive at this site. PDSI divisional data for Northern Virginia were obtained from NOAA
152 (https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp) in December 2017. Based on this, we
153 identified the three strongest droughts during the study period (Figs. **1, S1**; Table S1).

154 The droughts differed in intensity and antecedent moisture conditions (Fig. **S1**, Table S1). The 1966 drought
155 was preceded by two years of moderate drought during the growing season and severe to extreme drought
156 starting the previous fall. In August 1966, $PDSI$ reached its lowest monthly value (-4.82) of the three
157 droughts. The 1977 drought was the least intense throughout the growing season, and it was preceded by 2.5
158 years of near-normal conditions, making it the mildest of the three droughts. The 1999 drought was preceded
159 by wetter than average conditions until the previous June, but $PDSI$ plummeted below -3.0 in October 1998
160 and remained below this threshold through August 1999.

Data collection and preparation

162 Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree heights,
163 microenvironment characteristics, and species traits (Table 3). The SCBI ForestGEO plot was censused in

2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems $\geq$ 1cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species (Condit, 1998). From these census data, we used measurements of DBH from 2008 to calculate historical DBH and data for all stems $\geq$ 10cm to analyze functional trait composition relative to tree height (all analyses described below). Census data are available through the ForestGEO data portal (www.forestgeo.si.edu).

We analyzed tree-ring data (xylem growth increment) from 571 trees representing the twelve dominant species (Table 2; Fig. **S2**). Selected species were those with the greatest contributions to woody aboveground net primary productivity ($ANPP_{stem}$) and together comprised 97% of study plot $ANPP_{stem}$ between 2008 and 2013 (Helcoski et al., 2019). Cores (one per tree) were collected within the ForestGEO plot at breast height (1.3m) in 2010-2011 or 2016-2017. In 2010-2011, cores were collected from randomly selected live trees of each species that had at least 30 individuals $\geq$ 10 cm DBH (Bourg et al., 2013). Annual tree mortality censuses were initiated in 2014 (Gonzalez-Akre et al., 2016), and in 2016-2017, cores were collected from all trees found to have died since the previous year's census. We note that drought was probably not a cause of mortality for these trees, as monthly May-Aug $PDSI$ did not drop below -1.75 in these years or the three years prior (2013-2017), and that trees cored dead displayed similar climate sensitivity to trees cored live (Helcoski et al., 2019). Cores were sanded, measured, and crossdated using standard procedures, as detailed in (Helcoski et al., 2019). The resulting chronologies (Fig. **1a**) were published in Zenodo (DOI: 10.5281/zenodo.2649302) in association with Helcoski et al. (2019).

For each cored tree, we combined tree-ring records and allometric equations of bark thickness to reconstruct DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[r_{bark,2008} - r_{bark,Y} + \sum_{year=Y}^{2008} r_{ring,Y} \right]$$

Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark thickness. Bark thickness was estimated from species-specific allometries based on the bark thickness data from the site (Anderson-Teixeira et al., 2015b). Specifically, we used linear regression on log-transformed data to relate r_{bark} to diameter inside bark from 2008 data (Table S2), which were then used to determine r_{bark} in the DBH reconstruction.

Tree heights (H) were measured by several researchers for a variety of purposes between 2012 and 2019 (n=1,518 trees). Methods included direct measurements using a collapsible measurement rod on small trees (NEON, 2018) or a tape measure on recently fallen trees (this study); geometric calculations using clinometer and tape measure (Stovall et al., 2018a) or digital rangefinders (Anderson-Teixeira et al., 2015b; NEON, 2018); and ground-based LiDAR (Stovall et al., 2018b). Rangefinders used either the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error (Larjavaara and Muller-Landau, 2013), but in this instance there was no clear advantage of one or the other. Measurements from the National Ecological Observatory Network (NEON) were collected near the ForestGEO plot following standard NEON protocol, whereby vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a rangefinder (NEON, 2018). Species-specific height allometries were developed (Table S3) using log-log regression ($ln[H] \sim ln[DBH]$). For species with insufficient height data to create reliable species-specific allometries (n=2, JUNI and FRAM), heights were calculated from an equation developed by combining the height

202 measurements across all species. We then used these allometries to estimate H for each drought year, Y,
203 based on reconstructed DBH_Y. The distribution of H across drought years is shown in Fig. **S3**.

204 To characterize how environmental conditions vary with height, data were obtained from the NEON tower
205 located <1km from the study area via the neonUtilities package (Lunch et al., 2020). We used wind speed,
206 relative humidity, and air temperature data, all measured over a vertical profile spanning heights from 7.2 m
207 to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 (NEON,
208 2018). After filtering for missing and outlier values, we determined the daily minima and maxima, which we
209 then aggregated at the monthly scale.

210 Crown position–a categorical variable classifying trees based on exposure to sunlight–was recorded for all
211 cored trees that remained standing during the growing season of 2018 following the protocol of Jennings et al.
212 (1999). Trees were classified as follows: *dominant* trees were defined as those with crowns above the general
213 level of the canopy, *co-dominant* trees as those with crowns within the the canopy; *intermediate* trees as
214 those with crowns below the canopy level, but illuminated from above; and *suppressed* as those below the
215 canopy and receiving minimal direct illumination from above.

216 Topographic wetness index (TWI), used here as a metric of long-term mean moisture availability, was
217 calculated using the dynatopmodel package in R (Fig. **S2**) (Metcalfe et al., 2018). Originally developed by
218 Beven and Kirkby (1979), TWI was part of a hydrological run-off model and has since been used for a
219 number of purposes in hydrology and ecology (Sørensen et al., 2006). TWI calculation depends on an input
220 of a digital elevation model (DEM; ~3.7 m resolution from the elevatr package (Hollister, 2018)), and from
221 this yields a quantitative assessment defined by how "wet" an area is, based on areas where run-off is more
222 likely. From our observations in the plot, TWI performed better at categorizing wet areas than the Euclidean
223 distance from the stream.

224 Species' trait data were collected in August 2018 (Tables 2-3; Fig. **S4**). We sampled small, sun-exposed
225 branches up to eight meters above the ground from three individuals of each species in and around the
226 ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and
227 re-hydrated overnight in covered buckets under opaque plastic bags before measurements were taken.
228 Rehydrated leaves taken towards the apical end of the branch (n=3 per individual: small, medium, and
229 large) were scanned, weighed, dried at 60° C for $\geq$ 48 hours, and then re-scanned and weighed. Leaf area
230 was calculated from scanned images using the LeafArea R package (Katabuchi, 2019). LMA was calculated
231 as the ratio of leaf dry mass to fresh area. PLA_{dry} was calculated as the percent loss of area between fresh
232 and dry leaves. Wood density was calculated for ~1cm diameter stem samples (bark and pith removed) as
233 the ratio of dry weight to fresh volume, which was estimated using Archimedes' displacement. We used the
234 rapid determination method of Bartlett et al. (2012) to estimate osmotic potential at turgor loss point (π_{tlp}).
235 Briefly, two 4 mm diameter leaf discs were cut from each leaf, tightly wrapped in foil, submerged in liquid
236 nitrogen, perforated 10-15 times with a dissection needle, and then measured using a vapour pressure
237 osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by the osmometer was
238 used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ (Bartlett et al., 2012).

239 *Statistical Analysis*

240 For each drought year, we calculated a metric drought resistance (Rt) as the ratio of basal area increment
241 (BAI; *i.e.*, change in cross-sectional area) during the drought year to the mean BAI over the five years
242 preceding the drought (Lloret et al., 2011). Thus, Rt values <1 and >1 indicate growth reductions and

7

243 increases, respectively. Because the Rt metric could be biased by directional pre-drought growth trends, we
244 also tried an intervention time series analysis (ARIMA, (Hyndman et al., 2020)) that predicted mean
245 drought-year growth based on trends over the preceding ten years and used this value in place of the
246 five-year mean in calculations of resistance (Rt_{ARIMA}= observed BAI/ predicted BAI). The two metrics
247 were strongly correlated (Fig. **S5**). Visual review of the individual tree-ring sequences with the largest
248 discrepancies between these metrics revealed that Rt was less prone to unreasonable estimates than
249 Rt_{ARIMA}, so we selected Rt as our focal metric, presenting parallel results for Rt_{ARIMA} in the
250 Supplementary Info. In this study we focus exclusively on drought resistance metrics (Rt or Rt_{ARIMA}), and
251 not on the resilience metrics described in Lloret et al. (2011), because (1) we would expect resilience to be
252 controlled by a different set of mechanisms, and (2) the findings of (DeSoto et al., 2020) suggest that Rt is a
253 more important drought response metric for angiosperms in that low resistance to moderate droughts was a
254 better predictor of mortality during subsequent severe droughts than the resilience metrics.

255 Analyses focused on testing the predictions presented in Table 1 with Rt as the response variable, and then
256 repeated using Rt_{ARIMA} as the response variable. Models were run for all drought years combined and for
257 each drought year individually. The general statistical model for hypothesis testing was a mixed effects
258 model, implemented in the lme4 package in R (Bates et al., 2019). In the multi-year model, we included a
259 random effect of tree nested within species and a fixed effect of drought year to represent the combined
260 effects of differences in drought characteristics. Individual year models included a random effect of species.
261 All models included fixed effects of independent variables of interest (Tables 1,3) as specified below. All
262 variables across all best models had variance inflation factors <1.2 (1 +/- 0.019). We used AICc to assess
263 model selection, and conditional/marginal R-squared to assess model fit as implemented in the AICcmodavg
264 package in R (Mazerolle and portions of code contributed by Dan Linden., 2019). AICc refers to a corrected
265 version of AICc, and is best suited for small data sizes (see Brewer et al., 2016).

266 To avoid over-fitting models with five species traits (Table 3) across only 12 species, we did not include all
267 traits as fixed effects in a single linear mixed model, but rather conducted individual tests of each species
268 trait to determine the relative importance and appropriateness for inclusion in the main model. These tests
269 followed the model structure specified above, then added $ln[H]$ and $ln[TWI]$ to create a base model against
270 which we tested traits. Trait variables were considered appropriate for inclusion in the main model if they
271 had a consistent direction of response across all droughts and if their addition to the base model improved fit
272 (at $\Delta AICc \geq 1.0$) in at least one drought year (Table S4). We note that we did not use the $\Delta AICc \geq 1.0$
273 criterion as a test of significance, but rather of whether the variable had enough influence to be considered as
274 a *candidate* variable in full models.

275 We then determined the top full models for predicting Rt (or Rt_{ARIMA}). To do so, we compared models
276 with all possible combinations of candidate variables, including $ln[H]*ln[TWI]$ and species traits as specified
277 above. We identified the full set of models within $\Delta AICc=2$ of the best model (that with lowest AICc).
278 When a variable appeared in all of these models and the sign of the coefficient was consistent across models,
279 we viewed this as support for the acceptance/rejection of the associated prediction (Table 1). If the variable
280 appeared in some but not all of these models, and its sign was consistent across models, we considered this
281 partial support/rejection. In presentation of the results below, we note instances where the Rt_{ARIMA} model
282 disagreed with the Rt model, but otherwise do not discuss the Rt_{ARIMA} model.

283 All analysis beyond basic data collection was performed using R version 3.6.2 (R Core Team, 2019). Other
284 R-packages used in analyses are listed in the Supplementary Information (*Appendix S1*). All data, code, and

Results

Tree height and microenvironment

In the years for which we have vertical profiles in climate data (2016-2018), taller trees–or those in dominant crown positions– were generally exposed to higher evaporative demand during the peak growing season months (May-August; Fig. **2**). Specifically, maximum daily wind speeds were significantly higher above the top of the canopy (40-50m) than within and below (10-30m) (Fig. **2a**). Relative humidity was also somewhat lower during June-August, ranging from ~50-80% above the canopy and ~60-90% in the understory (Fig. **2b**). Air temperature did not vary consistently across the vertical profile (Fig. **2c**).

Crown position varied as expected with height (dominant > co-dominant > intermediate > suppressed), but with substantial variation (Fig. **2d**). There were significant differences in height across all crown position classes (Fig. **2d**). A comparison test between height and crown position data from the most recent ForestGEO census (2018) revealed a correlation of 0.73.

Community-level drought responses

At the community level, cored trees showed substantial growth reductions in all three droughts, with a mean Rt of 0.86 in 1966 and 1999, and 0.84 in 1977 (Fig. **2b**). Across the entire study period (1950-2009), the focal drought years were the three years with the largest fraction of trees exhibiting $Rt \leq 0.7$. Specifically, in each drought, roughly 30% of the cored trees had growth reductions of $\geq 30\%$ ($Rt \leq 0.7$): 29% in 1966, 32% in 1977, and 27% in 1999. However, some individuals exhibited increased growth, *i.e.*, $Rt > 1.0$: 26% of trees in 1966, 22% in 1977, and 26% in 1999.

In the context of the multivariate model, Rt did not vary across drought years. That is, drought year as a variable did not appear in any of the top models – *i.e.*, models that were statistically indistinguishable (ΔAICc<2) from the best model.

Tree height, microenvironment, and drought resistance

Taller trees (based on H in the drought year) showed stronger growth reductions during drought (Table 1; Figs. **4, S6**). Specifically, $ln[H]$ appeared, with a negative coefficient, in the best model ((ΔAICc=0) and all top models when evaluating the three drought years together (Tables S6-S7). The same held true for 1966 individually. For the 1977 drought, $ln[H]$ did not appear in the best model, but was included, with a negative coefficient, among the top models–*i.e.*, models that were statistically indistinguishable (ΔAICc<2) from the best model (Tables 1, S6-S7). For the 1999 drought, $ln[H]$ had no significant effect.

Rt had a significantly negative response to $ln[TWI]$ across all drought years combined (Figs. **4, S6**, Table S6-S7). The effect was also significant for 1977 and 1999 individually (Fig. **4**, Table S6). When Rt_{ARIMA} was used as the response variable, the effect was significant in 1977, and included in some of the top models in 1966 and 1999 (Table S7). This negates the idea that trees in moist microsites would be less affected by drought. Nevertheless, we tested for a $ln[H] * ln[TWI]$ interaction, a negative sign of which could indicate that smaller trees (presumably with smaller rooting volume) are more susceptible to drought in drier

324 microenvironments with a deeper water table. This hypothesis was rejected, as the $ln[H] * ln[TWI]$
325 interaction was never significant, and had a positive sign in any top models in which it appeared (Tables 1,
326 S6-S7). This term did appear with a positive coefficient in the best Rt_{ARIMA} model for all years combined
327 (Table S7), indicating that the negative effect of height on Rt was significantly stronger in wetter
328 microhabitats.

329 *Species' traits and drought resistance*

330 Species, as a factor in ANOVA, had significant influence (p<0.05) on all traits (wood density, LMA,
331 PLA_{dry}, and π_{tlp}), with more significant pairwise differences for wood density and PLA_{dry} than for LMA
332 and π_{tlp} (Table 2, Fig. **S4**). Drought resistance also varied across species, overall and in each drought year
333 (Fig. **3**). Significant differences in Rt across species were most pronounced in 1966 with a total of seven
334 distinct groupings, while 1977 had four and 1999 had two. Averaged across all droughts, Rt was lowest in
335 *Liriodendron tulipifera* (mean Rt = **0.66**) and highest in *Fagus grandifolia* (mean Rt = **0.99**).

336 Wood density, LMA, and xylem porosity were all poor predictors of Rt (Tables 1,S4-S5). Wood density and
337 LMA were never significantly associated with Rt in the single-variable tests and were therefore excluded
338 from the full models. Xylem porosity was also excluded from the full models, as it had no significant
339 influence for all droughts combined and had contrasting effects in the individual droughts: whereas
340 ring-porous species had higher Rt than diffuse- and semi-ring- porous species in the 1966 and 1999 droughts,
341 they had lower Rt in 1977 (Table S4). It is noteworthy that the two diffuse-porous species in our study,
342 *Liriodendron tulipifera* and *Fagus grandifolia*, were at opposite ends of the Rt spectrum (Fig. **3**), further
343 refuting the idea that xylem porosity is a useful predictor of Rt in the context of this study.

344 In contrast, PLA_{dry}, and π_{tlp} were both negatively correlated to drought resistance (Figs. **4, S6**; Tables
345 1,S4-S7). Both had consistent signs across all droughts, and their inclusion at least marginally improved the
346 model (ΔAICc > 1.0) for at least one of the three droughts (Table S4), qualifying them as candidate
347 variables for the full model. PLA_{dry} had a significant influence, with negative coefficient, in full models for
348 the three droughts combined and for the 1966 drought individually (Fig. **4**; Tables S6-S7). For 1977 and
349 1999, it was included with a negative coefficient in some of the top models (Tables S6-S7). π_{tlp} was included
350 with a negative coefficient in the best model for both all droughts combined and for the 1977 drought
351 individually (Fig. **4**; Table S6). It was also included in some of the top models for 1999 (Tables S6-S7).

Discussion

353 Tree height, microenvironment, and leaf drought tolerance traits shaped tree growth responses across three
354 droughts at our study site (Table 1, Fig. **4**). The greater susceptibility of larger trees to drought, similar to
355 forests worldwide (Bennett et al., 2015), was driven primarily by their height (Stovall et al., 2019). Taller
356 height was likely a liability in itself, and was also associated with greater exposure to conditions that would
357 promote water loss and heat damage during drought (Fig. **2**). There was no evidence that greater
358 availability of, or access to, soil water availability increased drought resistance; in contrast, trees in wetter
359 topographic positions had lower Rt (Zuleta et al., 2017; Stovall et al., 2019), and the larger potential rooting
360 volume of large trees provided no advantage in the drier microenvironments. The negative effect of height on
361 Rt held after accounting for species' traits, which is consistent with recent work finding height had a stronger
362 influence on mortality risk than forest type during drought (Stovall et al., 2020). Drought resistance was not
363 consistently linked to species' LMA, wood density, or xylem type (ring- vs. diffuse porous), but was

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negatively correlated with leaf drought tolerance traits (PLA_{dry}, π_{tlp}). This is the first study to our knowledge linking PLA_{dry} and π_{tlp} to growth reduction during drought. The directions of these responses were consistent across droughts (Table S6), supporting the premise that they were driven by fundamental physiological mechanisms. However, the strengths of each predictor varied across droughts (Fig. **4**; Tables S6-S7), indicating that drought characteristics interact with tree size, microenvironment, and traits to shape which individuals are most affected. These findings advance our knowledge of the factors that make trees vulnerable to growth declines during drought and, by extension, likely make them more vulnerable to mortality (Sapes et al., 2019).

The droughts considered here were of a magnitude that has occurred with an average frequency of approximately once every 10-15 years (Fig. **1a**, Helcoski et al., 2019) and had substantial but not devastating impacts on tree growth (Figs. **1b**). These droughts were classified as severe ($PDSI$ < -3.0; 1977) or extreme ($PDSI$ < -4.0; 1966, 1999) at our site and have been linked to tree mortality in the eastern United States (Druckenbrod et al., 2019). However, extreme, multiannual droughts such as the so-called "megadroughts" of this type that have triggered massive tree die-off in other regions (e.g., Allen et al., 2010; Stovall et al., 2019) have not occurred in the Eastern United States within the past several decades (Clark et al., 2016). Of the droughts considered here, the 1966 drought, which was preceded by two years of dry conditions (Fig. **S1**), severely stressed a larger portion of trees (Fig. **1b**). The tendency for large trees to have lowest resistance was most pronounced in this drought, consistent with other findings that this physiological response increases with drought severity (Bennett et al., 2015; Stovall et al., 2019). Across all three droughts, the majority of trees experienced reduced growth, but a substantial portion had increased growth (Fig. **1b**), consistent with prior observations that smaller trees can exhibit increased growth rates during drought (Bennett et al., 2015). It is likely because of the moderate impact of these droughts, along with other factors influencing tree growth (e.g., stand dynamics), that our best models characterize only a modest amount of variation in Rt: 11-12% for all droughts combined, and 18-25% for each individual drought (Fig. **S6**; Table S6).

Consistent with studies in other forests worldwide (Bennett et al., 2015), taller trees in this forest exhibited lower drought resistance. Mechanistically, this is consistent with, and reinforces, previous findings that biophysical constraints make it impossible for trees to efficiently transport water to great heights and simultaneously maintain strong resistance and resilience to drought-induced embolism (Olson et al., 2018; Couvreur et al., 2018; Roskilly et al., 2019). Taller trees also face dramatically different microenvironments (Fig. **2**). They are exposed to higher wind speeds and lower humidity (Fig. **2a-b**), resulting in higher evaporative demand. Unlike other temperate forests where modestly cooler understory conditions have been documented (Zellweger et al., 2019), particularly under drier conditions (Davis et al., 2019), we observed no significant variation in air temperatures across the vertical profile (Fig. **2c**). More critically for tree physiology, leaf temperatures can become significantly elevated over air temperature under conditions of high solar radiation and low stomatal conductance (Campbell and Norman, 1998; Rey-Sánchez et al., 2016). Under drought, when air temperatures tend to be warmer, direct solar radiation tends to be higher (because of less cloud cover), and less water is available for evaporative cooling of the leaves, trees with sun-exposed crowns may not be able to simultaneously maintain leaf temperatures below damaging extremes and avoid drought-induced embolism. Indeed, previous studies have shown lower drought resistance in more exposed trees (Liu and Muller, 1993; Suarez et al., 2004; Scharnweber et al., 2019). Unfortunately, collinearity between height and crown exposure in this study (Fig. **2d**) makes it impossible to confidently partition causality. Additional research comparing drought responses of early successional and mature forest stands,

along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

Belowground, taller trees would tend to have larger root systems (Enquist and Niklas, 2002), but this does not necessarily imply that they have greater access to or reliance on deep soil-water resources that may be critical during drought. While tree size can correlate with the depth of water extraction (Brum et al., 2019), the linkage is not consistent. Shorter trees can vary broadly in the depth of water uptake (Stahl et al., 2013), and larger trees may allocate more to abundant shallow roots that are beneficial for taking up water from rainstorms (Meinzer et al., 1999). Moreover, reliance on deep soil-water resources can actually prove a liability during severe and prolonged drought, as these can experience more intense water scarcity relative to non-drought conditions (Chitra-Tarak et al., 2018). In any case, the potentially greater access to water did not override the disadvantage conferred by height–and, in fact, greater moisture access in non-drought years (here, higher TWI) appears to make trees more sensitive to drought (Zuleta et al., 2017; Stovall et al., 2019). This may be because moister habitats would tend to support species and individuals with more mesophytic traits (Bartlett et al., 2016b; Mencuccini, 2003; Medeiros et al., 2019), potentially growing to greater heights (e.g., Detto et al. (2013)), and these are then more vulnerable when drought hits. The observed height-sensitivity of Rt, together with the lack of conferred advantage to large stature in drier topographic positions, agrees with the concept that physiological limitations to transpiration under drought shift from soil water availability to the plant-atmosphere interface as forests age (Bretfeld et al., 2018), such that tall, dominant trees are the most sensitive in mature forests. Again, additional research comparing drought responses across forests with different tree heights and water availability would be valuable for disentangling the relative importance of above- and belowground mechanisms across trees of different size.

The development of tree-ring chronologies for the twelve most dominant tree species at our site (Helcoski et al., 2019; Bourg et al., 2013) gave us the sample size to compare historical drought responses across species (Fig. **3**) and associated traits at a single site (see also Elliott et al., 2015). Our study reinforced current understanding (see Introduction) that wood density and LMA are not reliably linked to drought resistance (Table 1). Contrary to previous studies in temperate deciduous forests, we did not find an association between xylem porosity and drought resistance, as the two diffuse-porous species, *Liriodendron tulipifera* and *Fagus grandifolia*, were at opposite ends of the Rt spectrum (Fig. **3**). While the low Rt of *L. tulipifera* is consistent with other studies (Elliott et al., 2015), the high Rt of *F. grandifolia* contrasts with studies identifying diffuse porous species in general (Elliott et al., 2015; Kannenberg et al., 2019), and the genus *Fagus* in particular (Friedrichs et al., 2009), as drought sensitive. There are two potential explanations for this discrepancy. First, other traits can and do override the influence of xylem porosity on drought resistance. Ring-porous species are restricted mainly to temperate deciduous forests, while highly drought-tolerant diffuse-porous species exist in other biomes (Wheeler et al., 2007). *Fagus grandifolia* had intermediate π_{tlp} and low PLA_{dry} (Fig. **S4**), which would have contributed to its drought resistance (Fig. **4**; see discussion below). A second explanation of why *F. grandifolia* trees at this particular site had higher Rt is that the sampled individuals, reflective of the population within the plot, are generally shorter and in less-dominant canopy positions compared to most other species (Fig. **S4**). The species, which is highly shade-tolerant, also has deep crowns (Anderson-Teixeira et al., 2015b), implying that a lower proportion of leaves would be affected by harsher microclimatic conditions at the top of the canopy under drought (Fig. **2**). Thus, the high Rt of the sampled *F. grandifolia* population can be explained by a combination of fairly drought-resistant leaf traits, shorter stature, and a buffered microenvironment.

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Concerted measurement of tree-rings and leaf drought tolerance traits of emerging importance (Scoffoni et al., 2014; Bartlett et al., 2016a; Medeiros et al., 2019) allowed novel insights into the role of drought tolerance traits in shaping drought response. The finding that PLA_{dry} and π_{tlp} can be useful for predicting drought responses of tree growth (Fig. **4**; Table 1) is both novel and consistent with previous studies linking these traits to habitat and drought tolerance. Previous studies have demonstrated that π_{tlp} and PLA_{dry} are physiologically meaningful traits linked to species distribution along moisture gradients (Maréchaux et al., 2015; Fletcher et al., 2018; Medeiros et al., 2019; Simeone et al., 2019; Rosas et al., 2019; Zhu et al., 2018), and our findings indicate that these traits also influence drought responses. Furthermore, the observed linkage of π_{tlp} to Rt in this forest aligns with observations in the Amazon that π_{tlp} is higher in drought-intolerant than drought-tolerant plant functional type. Further, it adds support to the idea that this trait is useful for categorizing and representing species' drought responses in models (Powell et al., 2017). Because both PLA_{dry} and π_{tlp} can be measured relatively easily (Bartlett et al., 2012; Scoffoni et al., 2014), they hold promise for predicting drought growth responses across diverse forests. The importance of predicting drought responses from species traits increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that do not form annual rings, and for diverse tropical forests. Although progress is being made for the tropics (Schöngart et al., 2017), a full linkage of drought tolerance traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (Christoffersen et al., 2016; Powell et al., 2017).

As climate change drives increasing drought in many of the world's forests (Trenberth et al., 2014; Intergovernmental Panel on Climate Change, 2015), the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Our results show that taller, more exposed trees and species with less drought-tolerant leaf traits will be most affected, at least in terms of growth during the drought year. Resilience and survival are both linked to resistance (DeSoto et al., 2020; Gessler et al., 2020), implying that the same factors may influence these. Indeed, while the influence of PLA_{dry} and π_{tlp} on drought resilience and survival remains to be tested, taller trees have lower resilience (Trugman et al., 2018; Gillerot et al., 2020) and survival (Bennett et al., 2015; Stovall et al., 2019). As climate change-driven droughts affect forests worldwide, there is likely to be a shift from mature forests with tall, buffering trees to forests with a shorter overall stature (McDowell et al., 2020). At this point, species whose drought resistance relies in part on existence within a buffered microenvironment (e.g., *F. grandifolia*) could in turn become more susceptible. Here, the relative importance of tree height *per se* versus crown exposure becomes crucial, shaping whether the dominant trees of shorter canopies are significantly more drought resistant because of their shorter stature, or whether high exposure makes them as vulnerable as the taller trees of the former canopy. Studies disentangling the influence of height and exposure on drought tolerance will be critical to answering this question. Ultimately, distributions of tree heights and drought tolerance traits across broad moisture gradients suggest that forests exposed to more drought will ultimately shift towards shorter stature and be dominated by species with more drought-tolerant traits (Liu et al., 2019; Bartlett et al., 2016a; Zhu et al., 2018). Our study helps to elucidate the mechanisms behind these patterns, opening the door for more accurate forecasting of forest responses to future drought.

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Author Contribution

KAT, IM, and AJT designed the research. Tree-ring chronologies were developed by RH under guidance of AJT and NP. Trait data were collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.

Supplementary Information

Table S1: Monthly Palmer Drought Severity Index (PDSI), and its rank among all years between 1950 and 2009 (driest=1), for focal droughts.

Table S2: Species-specific bark thickness regression equations.

Table S3: Species-specific height regression equations.

Table S4. Individual tests of species traits as drivers of drought resistance, where Rt is used as the response variable.

Table S5. Individual tests of species traits as drivers of drought resistance, where Rt_{ARIMA} is used as the response variable.

Table S6. Summary of top full models for each drought instance, where Rt is used as the response variable.

Table S7. Summary of top models for each drought instance, where Rt_{ARIMA} is used as the response variable.

Figure S1. Time series of Palmer Drought Severity Index (PDSI) for the 2.5 years prior to each focal drought

Figure S2: Map of ForestGEO plot showing topographic wetness index and location of cored trees

Figure S3: Distribution of reconstructed tree heights across drought years.

Figure S4. Distribution of independent variables by species.

Figure S5. Comparison of Rt and Rt_{ARIMA} results, with residuals, for each drought scenario

Figure S6. Visualization of best model, with data, for all droughts combined.

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